A taxonomic treatment is presented for Hymenoxys subg. Macdougalia, which includes a single species, Hymenoxys higelovii. The treatment includes a discussion of the original circumscription of Hymenoxys higelovii (as Actinella higelovii), the later description of the genus Macdougalia to accommodate this taxon, and the eventual placement, based on chemical, cytological, and morphological evidence, of Macdougalia within Hymenoxys as a monotypic subgenus. The treatment also includes synonyms of Hymenoxys subg. Macdougalia and Hymenoxys higelovii, lectotypification of Actinella higelovii, and a description and range map for Hymenoxys higelovii.

Se presenta un tratamiento taxonómico de Hymenoxys subg. Macdougalia, que incluye una sola especie, Hymenoxys higelovii. El tratamiento incluye una discusión de la circunscripción original de H. higelovii (como Actinella higelovii), la descripción del género Macdougalia para acomodar este taxon, y la colocación eventual, basada en pruebas químicas, citológicas, y morfológicas, de Macdougalia en Hymenoxys como un subgénero monotípico. El tratamiento incluye también sinonimias de Hymenoxys subg. Macdougalia y Hymenoxys higelovii, lectotipificación de Actinella higelovii, y una descripción y mapa de distribución de Hymenoxys higelovii.

Hymenoxys Cass. subg. Macdougalia (A. Heller) Bierner comprises only one species, Hymenoxys higelovii (A. Gray) K.L. Parker. This taxon was originally described as Actinella higelovii A. Gray, Actinella Pers. being the generic name commonly used at that time (e.g., Torrey & Gray 1842) for taxa now placed in Tetraneuris Greene and Hymenoxys. When describing Actinella higelovii, Gray (1853) made no comments that would indicate any hesitation on his part as to its placement in Actinella.

Later (1883), when Gray positioned Actinella higelovii in Actinella section Hymenoxys, he commented, “Connects [section] Hymenoxys with [section] Euactinella, and with section Dugaldea [sic] of Helenium.” This statement indicates to me that Gray may not have been completely comfortable with his placement of this taxon. His section Hymenoxys equates today with Hymenoxys subg. Hymenoxys, Hymenoxys subg. Phileozera (Buckley) Cockerell (in part), and Hymenoxys subg. Picradenia (Hook.) Cockerell (Bierner 2001), his section Euactinella equates today with Tetraneuris, Hymenoxys subg. Phileozera (in
part), and *Hymenoxys* subg. *Rydergia* (Greene) Bierner (Bierner 2001; Bierner & Turner 2003), and his section *Dugaldea* (sic) of *Helinemium* equates today with *Hymenoxys* subg. *Dugaldia* (Cass.) Bierner (Bierner 2001).

Heller (1898) seems to have been even less sure about its placement, as indicated by his comment, "In habit it is more like the genus *Tetraneuris*, but has a different involucre, and while its involucre is somewhat similar to that of the genus *Picradenia* [= *Hymenoxys* subg. *Picradenia*], there is a wide difference in habit." His solution was to describe the genus *Macdougalia* to accommodate this one taxon, a circumscription followed by Cockerell (1904), Rydberg (1915), and Robinson (1981). Other workers, such as Turner and Powell (1977) and Karis and Ryding (1994), felt there was no clear basis for maintaining *Macdougalia* as a separate genus and submerged it in *Hymenoxys*.

Spring et al. (1994) began their study of chemical components of glandular trichomes in *Hymenoxys* and related genera by recognizing *Macdougalia* as a genus separate from *Hymenoxys*. By the end of the study they were of the opinion, based on sesquiterpene lactone and monoterpene glycoside chemistry, that *Macdougalia* should be incorporated into a broader concept of *Hymenoxys*. Likewise, Bierner and Jansen (1998), who began their study of DNA restriction site variation in *Hymenoxys* and related genera recognizing *Macdougalia* as a distinct genus, concluded that it is in fact congeneric with *Hymenoxys*. The relationship of *Macdougalia* to *Hymenoxys* is further supported by similarities of flavonoid chemistry (e.g., Wagner et al. 1972) and chromosome number, 2n = 30 being the chromosome number of *H. bigelovii* (Speese & Baldwin 1952; Strother 1966; Bierner unpublished and Parker & McClintock unpublished—see representative specimens) and the predominant number among the diverse taxa of *Hymenoxys* (e.g., Speese & Baldwin 1952; Beaman & Turner 1962; Strother 1966; Sanderson 1973; Turner et al. 1973). In 2001, Bierner formally recognized *Macdougalia* as a subgenus of *Hymenoxys*.

While Spring et al. (1994) were confident about the association of *Macdougalia* with *Hymenoxys*, they were less sure about its relationship to other taxa within *Hymenoxys*. The phenogram prepared from sesquiterpene lactone data placed *H. bigelovii* (as *Macdougalia bigelovii*) closest to *H. hoopesii* of subg. *Dugaldia* and *H. rushyi* of subg. *Picradenia*. The strict consensus tree prepared by Bierner and Jansen (1998) placed *H. bigelovii* (as *Macdougalia bigelovii*) in the clade containing taxa of *Hymenoxys* subg. *Dugaldia*, *Hymenoxys* subg. *Picradenia*, and *Hymenoxys* subg. *Plummera*, but no clear association with any species in particular was apparent.

Morphology also supports the placement of *Macdougalia* in *Hymenoxys*. The stems, peduncles, receptacles, ray florets, and disc florets of *Hymenoxys* *bigelovii* are very similar to those of the *Hymenoxys* species in general. Conversely, a substantial number of morphological differences support the recognition of *Macdougalia* as a subgenus.
Hymenoxys bigelovii usually has all simple leaves that are eglandular or sparsely glandular. Among the other taxa of Hymenoxys, only H. hoopesii has all simple leaves, and only H. texana has leaves that are weakly to moderately glandular (all of the other taxa have distinctly glandular leaves).

As in essentially all of the perennial taxa of Hymenoxys (and Tetraneuris as well), the basal leaf bases of H. bigelovii are persistent and tend to thicken the caudices distally as the plants age. The basal leaves of H. bigelovii, however, decay down to the veins so that the tops of the caudices usually appear to be encased in a stringy cocoon. I have observed this decay to the veins occasionally in other taxa of Hymenoxys, but it is unusual and never creates the appearance of a stringy cocoon.

The phyllaries of Hymenoxys bigelovii are in two unequal series, as they are in most of the taxa of Hymenoxys (those of subg. Dugaldia and subg. Rydbergia are in two or three subequal series). The outer phyllaries of H. bigelovii are basally connate only slightly to 1/5 their lengths; the outer phyllaries of the other Hymenoxys taxa with two unequal series (except for H. texana) are basally connate 1/4 to 2/3 their lengths. The inner phyllaries of H. bigelovii are narrowly lanceolate to narrowly obovate, have aristate apices, and very distinctly exceed the outer in length; inner phyllaries of the other Hymenoxys taxa with two unequal series are usually obovate, have acuminate to usually mucronate apices, and surpass the outer in length only slightly or not at all.

The relationship of Hymenoxys bigelovii to other taxa of Hymenoxys remains unclear. Its relatively large involucres (13–20 mm high by 23–32 mm wide) might suggest a connection to H. hoopesii, H. brandegeei, or H. grandiflora, but the phyllaries are very different. Perhaps a clue rests with some unusual populations of H. richardsonii var. richardsonii from Fremont County, Wyoming (e.g., Fisser 661 and 699 [RM], and Dorn 3516 [NY, RM]). The phyllaries look so much like those of H. bigelovii that I was convinced when I first saw the specimens that these plants represented an undescribed species belonging to subgenus Macdougalia, even though the plants had divided leaves (blades are only rarely divided into three segments in H. bigelovii) and were well separated geographically from H. bigelovii. When I was able to see them in the field, however, it was obvious that they are indeed plants of H. richardsonii var. richardsonii, but with narrower, longer, arista inner phyllaries. Yet, this illustrated to me that it is not a long morphologic leap from the involucres of H. bigelovii to those of some other Hymenoxys species.

TAXONOMY


Hymenoxys bigelovii (A. Gray) K.L. Parker, Madroño 10:159. 1950. BASIONYM: Actinella
Polycarpic perennials. Caudices sparingly branched, thickened distally, usually encased in a stringy coconu-like covering formed by the veins of the decaying leaf bases. Aerial stems 1-5, erect, usually unbranched distally, green throughout to purple-red-tinted distally to purple-red-tinted throughout, 20-70 cm, sparsely to densely pubescent, often tomentose proximally, eglandular or sparsely dotted with sessile glands. Leaves basal and cauline, alternate, linear to linear-lanceolate to linear-oblong-lanceolate, simple and entire or blades rarely divided into three segments, glabrous or sparsely to densely pubescent, eglandular or sparsely dotted with impressed glands; basal leaf bases expanded, clasping, persistent, sparsely to densely long-villous-woolly. Heads 1-5 per plant, usually borne singly but sometimes in panicle-forming arrays. Peduncles (1.5-)6-20(-29) cm, expanded apically, moderately to densely pubescent, densely tomentose distally beneath the involucres, sparsely to moderately dotted with sessile glands. Involucre hemispheric to broadly campanulate, 13-20 × 23-32 mm. Phyllaries in 2 series, outer phyllaries 13-19, basally connate only slightly to 1/5 their lengths, green throughout or yellow to yellow-green proximally and green distally, often purple-red tinted on the margins, lanceolate to narrowly lanceolate or obovate to narrowly obovate, 7-11 × 1.3-2.8 mm, weakly to moderately keeled, apices acute to acuminate, abaxial faces sparsely to densely pubescent, sparsely to moderately dotted with sessile and impressed glands, adaxial faces glabrous or sparsely pubescent, eglandular or sparsely dotted with sessile glands; inner phyllaries 13-18, free, bodies yellow to yellow-green and scale-like, usually green distally, often purple-red tinted at the apices, narrowly
lanceolate to narrowly obovate, 8.5–12.6 × (1.1–)1.5–2.2 mm, distinctly surpassing the outer, not keeled or weakly to moderately keeled, apices aristate, abaxial faces glabrous or sparsely pubescent, eglandular, adaxial faces glabrous, eglandular. Ray florets 13–15, pistillate, fertile; corollas yellow, extending well beyond the phyllaries, 13–26 × 5.4–9.5 mm, lobes 3, abaxial faces glabrous or sparsely pubescent, eglandular, adaxial faces glabrous, eglandular. Disc florets 100–250+, bisexual, fertile; corollas yellow, cylindric to cylindric campanulate, 5.7–7.4 × 0.7–0.9 mm, lobes 5, glabrous or sparsely pubescent, eglandular. Receptacles hemispheric to globose to ovoid, paleae none. Cypselae narrowly obpyramidal, 4.2–4.7 × 0.9–1.2 mm, densely pubescent with straight, forked, antrorse hairs, eglandular; pappi 9–11(-15), obovate–oblanceolate-aristate, 4.7–7.3 × 0.7–1.3 mm. Chromosome number, 2n = 30.

Flowering and Distribution.—Flowering May to June. Roadsides, edges of juniper-pine and pine forests, 1375–2470 m. Central to eastern Arizona and western New Mexico (Fig. 1).


Note.—More than 70 specimens were examined for this treatment. Those listed above were chosen as representative of the geographic distribution and morphologic variation of Hymenoxys bigelovii.

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